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2011

document version
Publisher's PDF, also known as Version of record

Link to publication in VU Research Portal

citation for published version (APA)
Lang, S. I. (2011). *Global change and the functional diversity of cryptogams in northern biomes*. [PhD-Thesis - Research and graduation internal, Vrije Universiteit Amsterdam]. Ipskamp Drukkers.

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Download date: 05. May. 2023

English summary

Global change and the functional diversity of cryptogams in northern biomes

Climate change in the (Sub)Arctic is expected to be more extreme and rapid compared to other regions on Earth. At these northern latitudes, cryptogams (bryophytes and lichens) are the dominant vegetation component both in terms of abundance and biodiversity, fulfilling important ecosystem functions such as regulation of hydrology, carbon balance, nitrogen fixation and preservation of permafrost. While responses of vascular plants to climate have been studied in much detail, cryptogams have been mostly neglected in these investigations. Here I present a detailed study on cryptogam responses to climate (change), focusing not only on their diversity and abundance in contrasting ecosystems, but also on the consequences these changes may have for the nutrient and carbon economy of the cryptogam community. I focus especially on nutrient cycling processes that are related to the 'afterlife effects' of traits of the cryptogams, through analyzing interspecific variation in nutrient resorption from senescing tissues, quality of the litter remaining and its consequent decomposability.

In chapter 2, peatland cryptogam and vascular plant responses to climate change, both in terms of temperature and soil moisture regimes, were investigated in subarctic Sweden (and partly in Norway), along natural climatic gradients, from micro- to macroscales, and within an *in-situ* warming experiment. Soil moisture and *Sphagnum* growth were significant drivers of vegetation composition, both at smaller and larger spatial scales along natural climatic gradients. The vegetation composition of peatlands within one region, however, was rather stable and not influenced by increasing temperatures. This finding was confirmed by the results of the warming experiment. However, the lack of effect of warming on the vegetation might also have been caused by the rather short-term experimental duration of four years. *Sphagnum* growth, determined by its position on the microgradient and temperature, was a useful tool in separating functional cryptogam groups since the abundances of lichens, liverworts, non-*Sphagnum* mosses and vascular plants were negatively related to *Sphagnum* abundance. Species richness and Shannon index of all cryptogams declined as *Sphagnum* increased in abundance towards the wetter parts of the gradient. This relation was not found for vascular plants, where sedges compensated for the loss of hummock species by increasing in the wetter parts of the

gradient. In conclusion, climate change impacts on subarctic peatlands are strongly determined by moisture and *Sphagnum* growth and, to a lesser extent, by shifts in temperature regimes. However, at the limits of current peatland distribution the positive effect of temperature on *Sphagnum* growth may result in an expansion of peatlands at higher elevations.

Responses of cryptogams and vascular species in (sub)arctic tundra (and forest) to climate change were investigated along two contrasting tundra transects in Alaska and northern Sweden. For these measurements I used the combination of both natural climatic gradients and warming experiments (chapter 3). Here, temperature was an important driver of plant community composition and species richness. Lichens strongly declined in response to higher temperature, followed by non-*Sphagnum* mosses and liverworts while *Sphagnum* showed a high resistance to temperature increases within the Alaskan warming experiment. Responses within experiments were more extreme at colder locations while below the treeline in the birch forest, hardly any changes were observed. Within the Swedish birch forest experiment, amount of litter was the only significant variable determining vegetation composition while soil ammonium was an additional variable in the Alaskan tundra experiment showing higher values in the control plots. Overall, especially dwarf shrubs but also the mosses *Sphagnum girgensohnii*, *Hylocomium splendens* and *Pleurozium schreberi* were positively related to warming, while the majority of cryptogams showed a negative relationship. These responses underlay the phenomenon of arctic greening observed over the last years in many parts of the Arctic. Differences between the two studies (chapter 2 and 3) on climate change and biodiversity were mainly due to the occurrence of a strong biotic driver in peatlands, *Sphagnum* growth, which regulated growth of most other vascular plants and cryptogams. Such a driver was not apparent in the tundra experiments and gradients.

The observed shifts in plant communities from cryptogam- to shrub-dominated tundra, may also affect related processes such as those related to nutrient cycles. In chapter 4, I therefore investigated nutrient resorption efficiencies (RE), i.e. the percentage of nutrients recycled from senescing tissue, in a wide range of cryptogams and vascular plants. In these analyses, I employed a novel method (Fourier transform infrared attenuated total reflectance; FTIR-ATR) to correct for mass loss during senescence based on structural chemistry which is not affected by the resorption process. Mosses, lichens and lycophytes generally showed low nitrogen RE (RE_N < 20%), liverworts and conifers an intermediate RE_N (40%) and monilophytes, eudicots and monocots a high RE_N (> 70%). For P, RE_P appeared higher in eudicots and liverworts than in mosses. Overall, increasing specialization in conducting tissue from cryptogams to vascular plants seemed to relate to increasing levels of RE. This broadly supported the idea that the evolution of conducting tissues towards specialized phloem has aided land plants to optimize not only their photosynthate transport during organ life, but also their internal nutrient recycling during organ senescence.

Once tissues have senesced, decomposition of the remaining litter will be initiated. To detect general patterns in potential decomposition rates among species and functional or taxonomical species groups, a wide range of mosses and lichens, typical and dominant in the subarctic flora, and a selection of vascular plants, were incubated simultaneously in a 2-year experiment in experimental garden litter beds in northern Sweden (chapter 5). Furthermore, their initial chemical traits determining mass loss rates were investigated. Lichens and vascular plants decomposed generally faster than bryophytes while within cryptogam taxa, species identity was an important determinant of mass loss rates. The exceptional role of *Sphagnum* was once more apparent when screening mass loss rates within bryophytes, as 2-year mass loss of *Sphagnum* mosses was consistently lower than for non-*Sphagnum* mosses or liverworts. The low decomposition rate of *Sphagnum* mosses is an important feature responsible for building up peatlands, but had never been demonstrated without the confounding effects of habitat variation. Using a subset of the large species set, I found that mass loss differed both among incubation environments (reflecting nutrient-rich and poor birch forest and *Sphagnum* peatlands, respectively) and species. The pattern of mass loss across incubation environments was not consistent among cryptogam species. Consequently, predictions about decomposition in the (Sub)Arctic should consider the influence of incubation environment, i.e. ecosystem type, on mass loss rates. Cryptogam mass loss could be predicted very well from infrared spectra (FTIR-ATR) of the initial chemical composition of primary and secondary compounds of the species. This technique thus provides a useful tool in predicting decomposition rates of a larger set of cryptogams. The initial macronutrient concentrations (N, P, carbon and cations) and initial litter pH, however, correlated less well with mass loss. This emphasizes the usefulness of including the complex mobile and structural chemistry, as done by FTIR-ATR, as a standard measurement when considering decomposition of cryptogams.

In the General Discussion (chapter 6), the relationships between cryptogam abundance and diversity changes in the (Sub)Arctic to processes concerning nutrient recycling, i.e. resorption and decomposition, are synthesized at different temporal, spatial or functional scales. Furthermore, additional aspects not covered in this thesis are highlighted. Future studies should include community-level biotic drivers such as species interactions, competition and facilitation, and evaluate how these affect abundance-weighted processes like decomposition rates. Also, direct climate effects on phenotypic expression of traits of a given species, and on decomposition rate might merit further study. Trophic interactions (herbivory) may counteract climate change-induced shifts in vegetation. Dispersal and reproduction processes will be important for species establishment and disappearance but have not been investigated yet for a larger cryptogam species set. On longer time scales, even evolutionary adaptations to environmental perturbations may be of interest. Shifts in vegetation composition due to climate change may also trigger changes in ecosystem effects of cryptogam species with respect to hydrology, carbon storage, permafrost insulation and N_2-fixation. The measurements conducted in this thesis will help us to identify the consequences of climate change for vegetation composition, specifically cryptogam composition, in the (Sub)Arctic at different temporal, spatial and functional scales. Furthermore, this thesis provides us with the necessary tools to develop predictions about the effects of these vegetation shifts onto ecosystem nutrient and carbon turnover.

In a nutshell we have learned: cryptogam species do matter!